

## AVIAN HABITAT ASSOCIATIONS IN RIPARIAN ZONES OF IDAHO'S CENTENNIAL MOUNTAINS

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**ABSTRACT.**—Patterns of bird distribution within riparian habitat of the Centennial Mountains, Idaho, were investigated during the summers of 1983–1984. Avian habitat use, vegetative structure, and saturated soil coverage were surveyed in 98, 0.25-ha plots. Avian abundance distributions and habitat relationships were plotted and compared with reciprocal averaging and canonical correlation analyses. Use of riparian habitats by avian species was non-random and indicated a correlation with vegetative structure, life form, and soil moisture. Canonical correlation analysis revealed that avian distributions paralleled a moisture gradient. Our results allow assessment of impacts on avian populations by environmental perturbations causing vegetative-structure and composition, or soil-moisture changes to riparian systems. These data indicate that subtle changes to riparian areas (e.g., from cattle grazing, timber harvest, drainage, etc.) may have severe impacts on the bird community. Received 9 July 1991, accepted 12 Feb. 1992.

Riparian habitats in western regions are severely threatened by numerous environmental perturbations, including development, forest-cutting practices, flood control, agriculture, grazing, and pollution (Kusler 1985). “Riparian vegetation has been referred to as the aorta of an ecosystem because of its significance to the perpetuation of water, fish, wildlife, rangeland, and forest resources” (Knopf and Samson 1988:77). Knopf and Samson (1988) also note that <1% of the western United States contains riparian vegetation, yet these habitats are used by more species of breeding birds than any other habitat type in North America. Detailed information on the various components of riparian ecosystems is needed to manage riparian habitats (Platts et al. 1987).

Bird distribution is often related to vegetative characteristics or habitat types, which are a subset of the overall “niche gestalt” (James 1971). Vegetative structure may provide proximal factors for habitat selection (Hilden 1965). In turn, this habitat selection process provides ultimate factors such as food, nest sites, and protection from predators (Hilden 1965, Balda 1975). Causal relationships between habitats and birds are difficult to determine, since habitat characteristics perceived by bird species for habitat selection are usually unknown, and analyses of field data only reveal correlations or associations (Johnson 1981a, Karr 1981).

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Examinations of avian-habitat relationships often have incorporated aspects of vegetative structure and plant species composition, which then are correlated with bird community structure (Carothers et al. 1974, Willson 1974, Stamp 1978, Stauffer and Best 1980, Meents et al. 1981) or with the abundance of singing males (James 1971, Whitmore 1975, Smith 1977). Moisture gradients and vegetative physiognomy also may be correlated with avian distribution (Smith 1977, Swift et al. 1984). Interactions of water with various physical characteristics of the environment (e.g., topography, soil, elevation) contribute to the diversity of riparian vegetation (Thomas et al. 1979). Furthermore, riparian ecosystems are highly productive and support a greater faunal diversity when compared to adjacent uplands (Odum 1978).

Our objectives were to sample and analyze avian habitat use within the riparian zones of the Centennial Mountains, and to sample and describe riparian habitat gradients and examine distributions of avian abundance among habitats. We sought to determine if different physiognomic characteristics within the riparian zone reflected different use of various riparian habitats by bird species.

#### STUDY AREA AND METHODS

The study was conducted in the eastern portion of the Centennial Mountains, Fremont and Clark counties, Idaho (see maps in Douglas and Ratti 1984). Elevation on the study area ranged from approximately 1860 to 1940 m. Lodgepole pine (*Pinus contorta*) was the most abundant tree species, and forest stands had extensive mountain pine beetle (*Dendroctonus ponderosae*) infestation. Engelmann spruce (*Picea engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*) dominated narrow, V-shaped drainages. Quaking aspen (*Populus tremuloides*) occurred in small stands along lower slopes. Willows (*Salix myrtilifolia*, *S. drummondiana*, *S. geyeriana*, *S. wolfii*, and *S. phylicifolia*) dominated shrub communities. Willow communities were found at moist sites, and understory composition ranged from relatively xerophytic mixed graminoids and forbs to mesophytic *Carex* spp. Many sites with saturated soils were occupied entirely by water sedge (*Carex aquatilis*), Ross sedge (*C. rostrata*), and short-beaked sedge (*C. simulata*) and did not support woody vegetation. Beaver (*Castor canadensis*) dams caused inundation of portions of the riparian zone.

*Plot establishment.*—During May and June 1983, 98 study plots were established within 20 riparian drainages described by Youngblood et al. (1985). Plots (35 × 71.5 m, 0.25 ha) were placed at 250-m intervals with the long axis parallel to the general compass bearing of the drainage. Plots were randomly placed perpendicular to the drainage within the riparian zone. A maximum of three plots was placed in drainages with homogeneous vegetative composition, i.e., as opposed to most drainages with heterogeneous vegetative communities. This method was devised to prevent excess sampling of one vegetative type in a large drainage and to provide relatively representative sampling of drainages with widely varying lengths and widths.

*Avian censusing.*—Each plot was censused six times in 1983 and twice in 1984 by one observer for 30 min between sunrise and noon. Presence, number, and location of all individuals of all bird species were recorded. Censusing occurred daily during 10-day intervals separated by four days from 8 June through 21 July 1983, and from 5 July through

2 September 1984 (late spring snow melt prevented June censusing in 1984). Observers and census times were rotated among plots within the sampling periods. Bird observations were classified by vegetative substrate (i.e., habitat components) as conifer, aspen, snag, willow, dry meadow, moist meadow, bog, in or adjacent to water, flight, and "other." Relative percent of observations was calculated for both the habitat components (e.g., snags) and the habitat regions (see Results, e.g., conifer-dominated) by dividing the total number of observations in each category for each species by the total number of observations for each species ( $\times 100$ ). Unidentified birds or birds flying over a plot were omitted from the analyses. We were careful to record specific individual birds only once on each plot. Birds were not censused during periods of severe wind or rain (Robbins 1981).

*Vegetation sampling.*—Plots were sampled for vegetative volume during July and August (89 plots in 1983, 9 in 1984). Higher elevation plots were sampled later in the season to record greatest vegetation cover. Vegetative volume of all plant species and the volumes of the two dominant species ( $>5\%$  cover) were measured at 0.3, 0.9, 1.8, and 3.0 m using coverboard techniques (MacArthur and MacArthur 1961, Hayes et al. 1981) at 16 systematically positioned points within each plot (transects originating at each point were alternated and evenly distributed among cardinal directions). Foliage volume was recorded as zero for a given sample point and height if the distance between the observer and coverboard was  $>15.2$ . Eight volume variables were calculated from the data for each plot: (1) low graminoid (0.3 m), (2) high graminoid (0.9 m), (3) low forb (0.3 m), (4) high forb (0.9 m), (5) low willow (0.3 + 0.9 m), (6) high willow (1.8 + 3.0 m), (7) low conifer (0.3 + 0.9 m), and (8) high conifer (1.8 + 3.0 m). Saturated soil was estimated within a 1-m<sup>2</sup> quadrat centered in each sample plot and was recorded as saturated or not saturated. Soils were considered saturated if water ran into a depression made by a footprint.

*Data analyses.*—A reciprocal averaging algorithm (RA) (Hill 1973) in the program ORDIFLEX (Gauch 1977) was used to position the 98 plots along multifactorial habitat gradients from square root-transformed variables. Reciprocal averaging is considered superior to principal component analysis (PCA) for data sets containing long community gradients (Gauch 1982). Study plot scores and habitat variable scores found by RA will maximize the correlation between them. Study plots were graphed across the first RA axes based on their ordination scores. Plots most similar with respect to habitat variables were positioned relatively closely, i.e., the degree of dissimilarity among plots was reflected by increasing separations. Environmental interpretation of two-dimensional habitat space was investigated by plotting values of the original habitat variables across the RA axes. This led to a subjective partitioning of six general riparian habitat regions (see Results). The regions represent riparian vegetative communities and were characterized by averaging the habitat variables across study plots located within each partitioned area.

Percents of observations of avian species using each study plot was superimposed onto the habitat space. Percentages were summed within each of the six habitat regions and then proportioned into the environmental categories corresponding to the bird's location when initially observed (e.g., conifer, willow, snag, bog, etc.).

The Shannon-Weaver information equation (Shannon and Weaver 1949) was used to measure habitat breadth for each bird species for the six habitat regions (Johnson 1977). The proportions of avian observations were not scaled with respect to the number of study plots in each region. Thus, habitat breadths were not escalated for species regularly using abundant habitats (Rotenberry and Wiens 1980).

Avian relative frequency (percentages) values and the nine habitat variables were square-root transformed and used in a canonical correlation analysis (CCA) for all plots (Hotelling 1936). Interpretations of habitat canonical variates were derived from correlations with original habitat variables (Levine 1977, Gittens 1979, Smith 1981).

TABLE 1  
HABITAT BREADTH<sup>a</sup> AND PERCENTAGE<sup>b</sup> OF BIRD OBSERVATIONS IN RIPARIAN HABITAT  
REGIONS OF THE CENTENNIAL MOUNTAINS, IDAHO, SUMMER 1983–1984

Species (N)	Habitat breadth	Habitat regions <sup>c</sup>					
		I	II	III	IV	V	VI
Common Snipe (89)	1.48	2.3	10.1	10.1	23.6	10.1	43.8
Red-naped Sapsucker (46)	0.89	0	6.5	26.1	0	65.2	2.2
Willow Flycatcher (65)	0.94	0	0	15.4	0	60.0	24.6
Tree Swallow (655)	1.34	0.1	7.0	7.2	9.2	40.0	36.5
Mountain Chickadee (84)	1.36	28.6	11.9	40.5	2.4	16.6	0
American Robin (237)	1.44	11.4	7.2	23.2	1.7	45.6	10.9
Warbling Vireo (104)	0.95	8.7	0	12.5	0	69.2	9.6
Yellow Warbler (436)	1.16	0.2	3.2	16.7	1.6	54.4	23.9
Yellow-rumped Warbler (105)	1.43	30.5	15.2	25.7	0	26.7	1.9
MacGillivray's Warbler (71)	0.77	2.8	0	26.8	0	69.0	1.4
Common Yellowthroat (169)	0.57	0	0	3.0	4.1	7.7	85.2
Wilson's Warbler (109)	0.86	1.8	0	12.9	0	70.6	14.7
Western Tanager (66)	1.36	33.3	10.6	37.9	0	15.2	3.0
Song Sparrow (116)	0.97	0	1.7	19.0	0	16.4	62.9
Lincoln's Sparrow (496)	1.55	3.4	10.9	22.6	4.2	28.8	30.1
White-crowned Sparrow (227)	0.96	4.4	0	18.9	0	66.1	10.6
Dark-eyed Junco (152)	1.37	34.9	12.5	40.1	1.3	8.6	2.6
Red-winged Blackbird (329)	1.33	0	11.3	17.9	23.7	1.8	45.3
Brown-headed Cowbird (90)	1.53	13.3	5.6	23.3	1.1	32.2	24.5
Pine Siskin (462)	1.34	18.0	1.9	29.9	0	40.0	10.2

<sup>a</sup> Shannon-Weaver (1949) index.

<sup>b</sup> The number of observations in each habitat component divided by N for each species  $\times$  100.

<sup>c</sup> I = conifer dominated, II = mesic meadow/conifer edge, III = composite communities, IV = mesic meadow, V = tall willow/xeric, and VI = short willow/mesic.

Consistency among observers, and between-year variation of habitat use by avian species, and study-plot use by individual species was investigated. To test for differences among three observers in the 1983 census, counts for 20 of the most abundant species (Table 1) were divided by the total number of birds observed, arc-sine transformed, and subjected to multivariate analysis of variance (Morrison 1976). Annual change in avian habitat use was investigated using the McNemar test (Conover 1980) and data from 81 plots sampled by a single observer (DCD) in 1983 and 1984. Sorenson's similarity index (Sorenson 1948, in Mueller-Dombois and Ellenberg 1974) was used to test for differences in an individual species' use of study plots between years. To test these differences, the original similarity index was compared to the distribution of 100 indices generated from random subsets of the original data (Garratt and Steinhorst 1976, Lawlor 1980). Statistical tests were judged significant with alpha levels  $<0.05$ .

## RESULTS

We obtained 4817 observations of 77 bird species. However, we restricted our statistical analysis to 20 species that were observed during



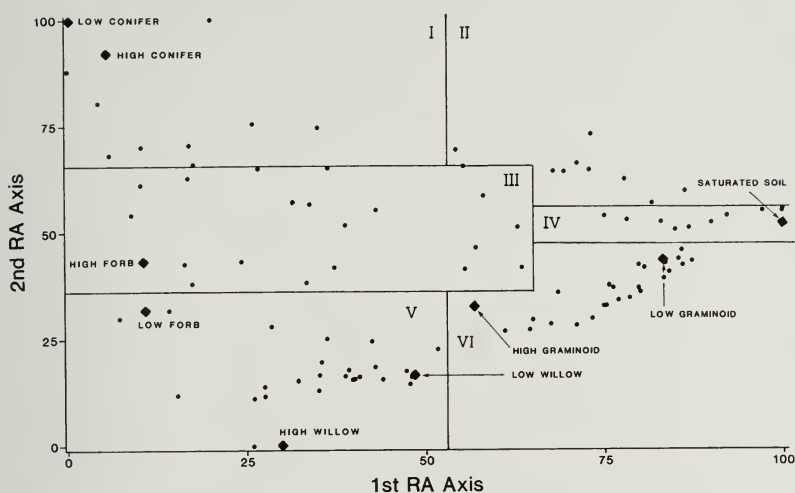


FIG. 1. Ordination of study plots (dots) and habitat variables by reciprocal averaging of riparian zones, Centennial Mountain, Idaho, 1983 and 1984. Regions were classified as: I = conifer dominated, II = mesic meadow/conifer edge, III = composite communities, IV = mesic meadow, V = tall willow/xeric, and VI = short willow/mesic.

>2 census periods on >10 plots (Table 1). This restriction insured adequate sample size for analysis and eliminated rare or transient species.

*Environmental gradients.*—The first RA axis, primarily a moisture gradient, accounted for 41.4% of the total variation in vegetative structure (Fig. 1). The second RA axis explained an additional 28.3% of variation and separated communities dominated by conifer and willow. Other axes were not considered in the analysis. The habitat variables were positioned along an inverted arch (Fig. 1) that resulted from non-linear relationships among the variables (Phillips 1978, Gauch 1982, Meents et al. 1981). Although the second axis does not convey information independent of the first axis, its inclusion in the analysis enhanced separation of study plots and improved environmental interpretation.

The two-dimensional RA ordination was divided into six riparian habitat regions (Fig. 1). Regions on the left included more xeric plots compared to plots on the right that had high coverage of saturated soils (Fig. 2). Region I included plots found in narrow, V-shaped and “conifer-dominated” riparian zones (Figs. 1 and 2). Typical community types (sensu Youngblood et al. 1985) within region I were *Picea/Cornus stolonifera* and *Picea/Galium triflorum*. Some narrow, patchy bands of willow communities were present on stream courses in this region. Plots in region II, “mesic meadow/conifer edge,” were mesic meadow commu-

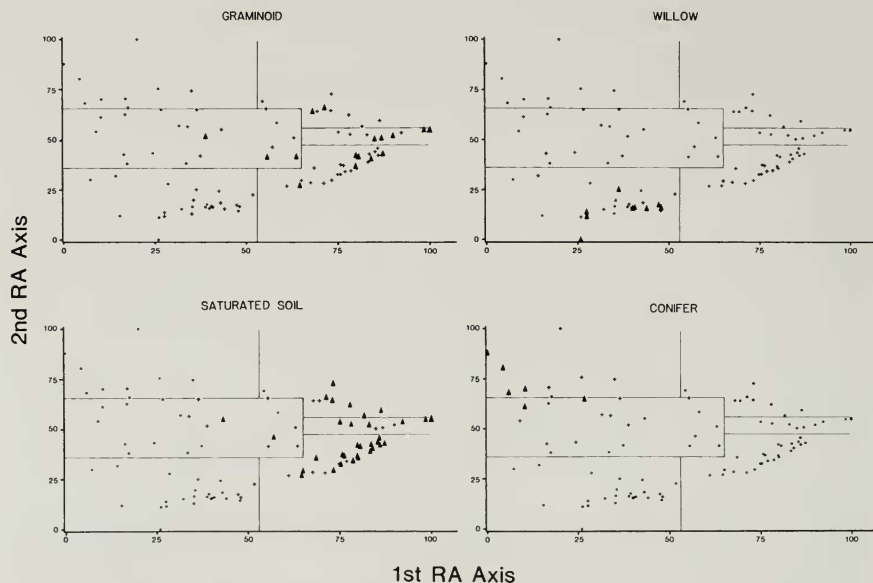


FIG. 2. Overlay of four habitat variables on the reciprocal averaging ordination of riparian zones, Centennial Mountains, Idaho, 1983 and 1984. Dots represent plots where the relative value of the variable was 0–25%, + symbols indicate plots 26–75%, and triangles indicate plots with relative values 75–100% of the largest observation recorded.

nities similar to region IV but were bordered by *Pinus contorta* communities and generally did not contain *Salix* spp. Plots in region III, “composite community,” were heterogeneous and composed of both conifer and willow-dominated communities. These plots were typical of narrow riparian zones where willow communities were bounded by coniferous forests. Plots in region IV, “mesic meadow,” were dominated by meadow communities with high graminoid coverage (Fig. 2) similar to the *Carex rostrata*, *C. aquatilis* and *C. nebrascensis* community types of Youngblood et al. (1985). These plots were composed primarily of *Carex* spp. and were often too wet to support woody species. Plots in regions V, “tall willow/xeric,” and VI, “short willow/mesic,” contained *Salix*-dominated communities (e.g., *Salix geyeriana*/*Carex rostrata*, *S. wolfii*/*C. aquatilis* and *S. wolfii*/*C. rostrata* community types of Youngblood et al. 1985). Taller, well-developed *Salix* canopies (Fig. 2) with understories of mixed grasses and forbs (e.g., *S. boothii*/*Smilacina stellata* community type of Youngblood et al. 1985) were found in plots of region V. Lower-stature, open-canopy *Salix* communities with *Carex* understories were found in region VI plots (Fig. 2). These habitats were common in drainages dammed and inundated by beaver.

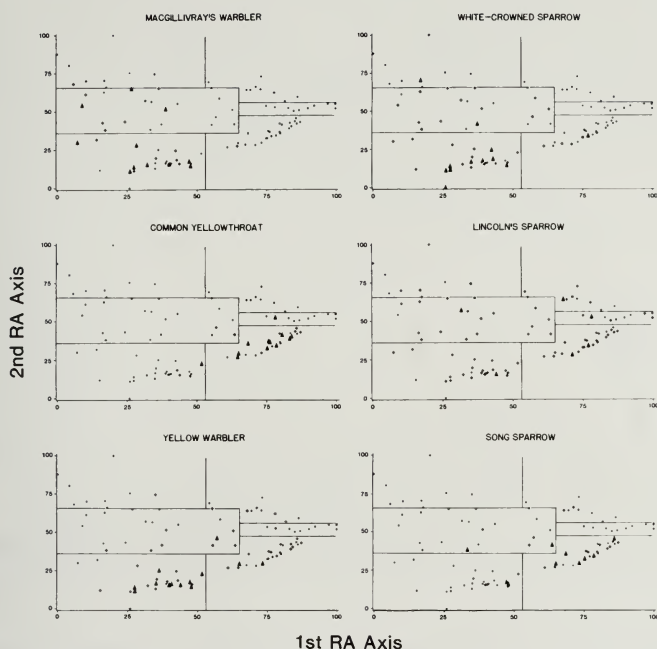


FIG. 3. Overlay of the relative frequency (percentage) of observation for six bird species on the reciprocal averaging ordination of riparian zones, Centennial Mountains, Idaho, 1983 and 1984. Dots represent plots with no observations, + symbols indicate plots with the relative frequency of observation < 3%, and triangles indicate plots with a relative frequency > 3%.

Separation of study sites across the second RA axis diminished as saturated soil coverage increased along the first RA axis (Fig. 2). This represented the lack of woody vegetation in the mesic meadow plots. In mesic regions, willow communities generally were low-structured and coniferous stands were decadent. As sites became more xeric, both willow and conifer communities tended to be more vigorous and productive. Thus, the contrast between willow and conifer foliage volumes was greater across the xeric portions of the moisture gradient (Fig. 2). The RA distribution of habitat variables and selected bird species may be compared by cross reference of Figs. 2 and 3.

The first habitat canonical variate was negatively correlated with saturated soil coverage, and the second variate was positively correlated with willow foliage volume. Again, an arch distortion resulted from the addition of the second axis and non-linear relationships among the variables. Interpretation was viewed across the single curved axis: a gradation from mesic meadows, into mesic short-willow communities, into xeric tall-

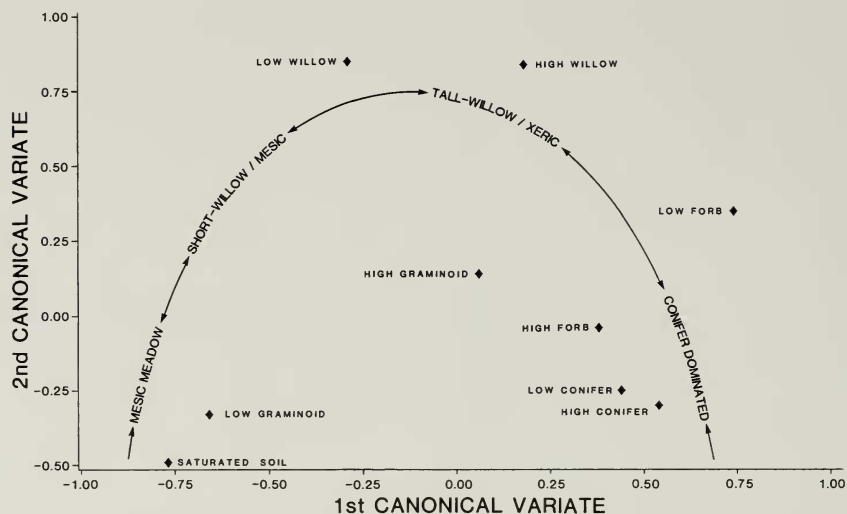


FIG. 4. Positions of the eight habitat variables on the first and second canonical correlation axes and the habitat gradient, Centennial Mountains, Idaho, 1983 and 1984.

willow communities, and finally into a conifer-dominated zone (Fig. 4). This arch, when inverted, was very similar to the RA ordination of habitat variables (Fig. 1). For similar analytical comparisons see Gauch (1982).

*Avian-habitat associations.*—Interdependency of the avian and habitat data sets was evident as variation in avian distributions paralleled vegetative composition along a moisture gradient. The first and second habitat variates accounted for 16% and 13%, respectively, of the standardized variance in the avian data set. The spatial arrangement of the bird species reflected their associations with the curved habitat axis (Fig. 5). The Common Snipe (*Capella gallinago*) and Red-winged Blackbird (*Agelaius phoeniceus*) were associated with wet meadow habitats. The Common Yellowthroat (*Geothlypis trichas*), Song Sparrow (*Melospiza melodia*), Tree Swallow (*Tachycineta bicolor*), and Lincoln's Sparrow (*M. lincolni*) showed affinities with the mesic short-willow communities. The White-Crowned Sparrow (*Zonotrichia leucophrys*), MacGillivray's Warbler (*Oporornis tolmiei*), Warbling Vireo (*Vireo gilvus*), and Red-naped Sapsucker (*Sphyrapicus nuchalis*) occupied the xeric tall-willow portion of the gradient. The Willow Flycatcher (*Empidonax traillii*), Yellow Warbler (*Dendroica petechia*), and Wilson's Warbler (*Wilsonia pusilla*) were intermediate in their association with the mesic and xeric willow habitats. The Yellow-rumped Warbler (*Dendroica coronata*), Dark-eyed Junco (*Junco hyemalis*), Mountain Chickadee (*Parus gambeli*), and Western Tanager (Pi-



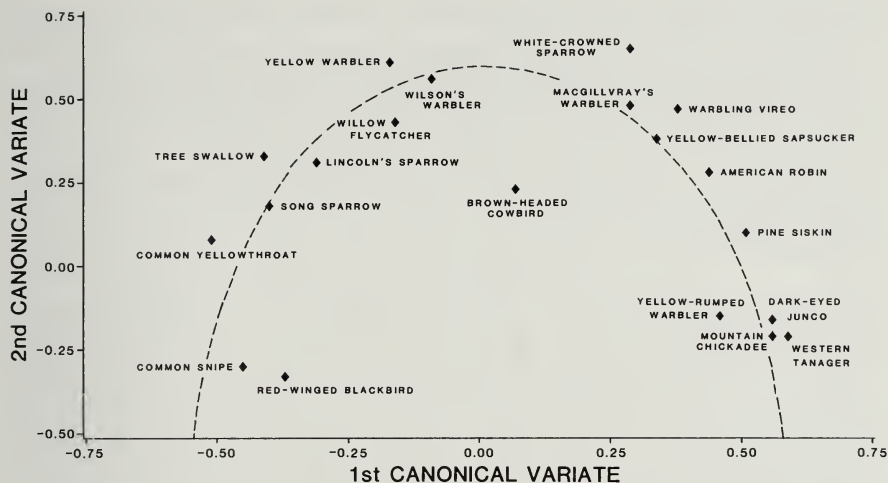


FIG. 5. Positions of 20 avian species variables on the first and second canonical correlation axis, Centennial Mountains, Idaho, 1983 and 1984.

*ranga ludoviciana*) were associated with the conifer-dominated areas, and the American Robin (*Turdus migratorius*) and Pine Siskin (*Carduelis pinus*) were intermediate with respect to their association with conifer and tall-willow habitats. The Brown-headed Cowbird (*Molothrus ater*) was not correlated with either axis and was centrally positioned, indicating a non-discriminating distribution.

Common Yellowthroats were observed in mesic habitats that supported low-structured willow and dense graminoid understories (Fig. 3). This species' specificity with mesic, short-willow communities (85.2% and 87.5% of 169 observations, Tables 1 and 2, respectively) resulted in its very low index of habitat breadth (Table 1). Common Yellowthroat observations were rare outside the short-willow-mesic habitat.

In contrast, the MacGillivray's Warbler occurred in xeric willow communities, primarily tall willows with mixed graminoid and forbs (Fig. 3, Table 1). Willow-conifer composite habitats (Region III) also were used by MacGillivray's Warbler, again across the more xeric portions. Compared to other species, the MacGillivray's Warbler was a specialist with respect to use of riparian habitat (i.e., willows, Table 2), which is also reflected by the low habitat breadth value (Table 1).

The Yellow Warbler displayed a general use of willow-dominated habitats (Fig. 3). Observations extended across the moisture gradient from xeric tall-willow communities into mesic short-willow habitat (Table 1). Yellow Warblers were associated with composite communities near the

TABLE 2  
PERCENTAGE OF BIRD OBSERVATIONS ACROSS NINE RIPARIAN HABITAT COMPONENTS  
DURING THE SUMMER OF 1983-1984, CENTENNIAL MOUNTAINS, IDAHO

Species (N)	Habitat components <sup>a</sup>								
	Cf	As	Sn	Wl	DM	MM	Bg	Wa	Fl
Common Snipe (89)	1.1	0	7.9	12.4	1.1	0	58.4	1.1	18.0
Red-naped Sapsucker (46)	13.0	15.2	26.1	32.7	0	0	0	0	13.0
Willow Flycatcher (65)	6.2	6.1	12.3	66.1	0	0	0	0	9.3
Tree Swallow (655)	0	1.1	5.9	0.6	0	0	0.7	0	91.7
Mountain Chickadee (84)	76.2	3.6	16.7	0	0	0	0	0	3.5
American Robin (237)	14.3	8.0	39.4	7.6	0	4.7	2.5	1.7	21.8
Warbling Vireo (104)	18.3	29.8	6.7	34.6	0	0	0	0	10.6
Yellow Warbler (436)	8.7	5.3	13.8	60.1	0	0	0	0	11.7
Yellow-rumped Warbler (105)	60.0	1.9	14.3	12.4	0	0	0	0	11.4
MacGillivray's Warbler (71)	9.8	2.8	4.2	73.3	0	0	0	0	8.5
Common Yellowthroat (169)	0	0	2.4	87.5	0	0	0	0	10.1
Wilson's Warbler (109)	6.4	0	5.5	79.9	0	0	0	0	8.2
Western Tanager (66)	59.2	3.0	22.7	4.6	0	0	1.5	0	9.0
Song Sparrow (116)	5.9	0	13.9	71.6	0	0	0.9	2.6	5.1
Lincoln's Sparrow (496)	12.5	1.2	14.9	55.9	0	1.8	1.8	0.6	10.9
White-crowned Sparrow (227)	16.4	6.2	15.9	53.7	0.9	1.3	0	0	5.6
Dark-eyed Junco (152)	43.4	0.7	25.6	5.9	0	3.3	3.3	2.0	15.8
Red-winged Blackbird (329)	6.1	0	37.0	16.2	0	0	25.2	0.6	14.9
Brown-headed Cowbird (90)	15.5	3.3	67.8	11.2	0	0	0	0	2.2
Pine Siskin (462)	30.7	9.2	36.2	5.4	0	3.5	1.4	0.4	13.2

<sup>a</sup> Cf = conifer, As = aspen, Sn = snag, Wl = willow, DM = dry meadow, Bg = bog, Wa = water, and Fl = flight.

peripheries of willow-dominated habitats, as well as with snags and conifers adjacent to wet meadows (Regions II and IV, Tables 1 and 2). Compared to the previous two species, the Yellow Warbler had a greater habitat breadth (Table 1) and greater diversity of associated environmental components (Tables 1 and 2).

Song, White-crowned, and Lincoln's sparrows had habitat associations similar to the warbler species. The Song Sparrow exploited primarily mesic short-willow communities (Fig. 3, Table 1) and was observed most

commonly in willows (Table 2). The White-crowned Sparrow was generally observed in xeric habitats, predominantly tall willow, but also composite communities (Fig. 3, Table 1). White-crowned Sparrow use of conifer, quaking aspen, and snags was more extensive than that of the Song Sparrow (Table 2). Lincoln's Sparrows were the most widely distributed species among study plots. The very generalized distribution across riparian habitats (Fig. 3, Table 1) for Lincoln's Sparrow corresponded with a high index of habitat breadth (Table 1) and a high diversity of use of environmental components (Table 2).

*Between-year variation.*—Eight of the 10 analyses of variance indicated significant ( $P < 0.05$ ) observer variability during the 1983 season. Thus, between-year variations in avian habitat use were compared with data collected by the observer common to both field seasons. Balanced sampling intensity by the common observer across years occurred at 81 plots (2 censuses/plot/year), so subsequent analyses were restricted to data collected at those plots. Wilson's Warbler was the only species that showed significant changes in distribution between years. This warbler used nine plots in 1983 that were not used during 1984. Conversely, only one plot was unique to the 1984 season. The McNemar test indicated a decrease ( $P < 0.05$ ) from 1983 to 1984 in the number of sites used by Wilson's Warbler. This species did not display a shift in the type of riparian habitat used, but rather its range of distribution in 1984 was more restricted.

The hypothesis that study plots used in 1983 had zero similarity with those used in 1984 was not rejected ( $P > 0.05$ ) for the Brown-headed Cowbird, Red-naped Sapsucker, Western Tanager, and Yellow-rumped Warbler. The Brown-headed Cowbird again displayed nonspecificity and was the only species observed at completely different study plots between years. Brown-headed Cowbird observations were scattered across habitat regions in 1983, but confined more to willow-dominated areas in 1984. The Red-naped Sapsucker, Western Tanager, and Yellow-rumped Warbler were observed at more sites in 1984, and all three species showed greater use of xeric tall-willow communities during the year.

#### DISCUSSION

Avian-habitat associations were influenced primarily by vegetative composition which was influenced primarily by soil moisture. Swift et al. (1984) reported that surface hydrology was a dominant factor affecting the plant and animal community in a Massachusetts wetland forest. In an Ozark Mountain watershed, avian distribution was correlated with vegetation physiognomy that paralleled a moisture gradient (Smith 1977). In both our RA and CCA analyses, the relationship between soil moisture and vegetation was reflected in the first habitat axis. Although this axis

portrayed a moisture gradient, it also incorporated the interdependencies between soil moisture and vegetative composition that are inherent in the analysis.

Many of the riparian bird species had discrete patterns of distribution along the moisture gradient. Such "displacement patterns" across resource axes may provide evidence that competition influences bird community composition (Cody 1974). The Song Sparrow used short-willow communities growing on mesic soils, while the closely related White-crowned Sparrow exploited xeric, tall-willow habitats (Table 1). The Common Yellowthroat occurred in short-willows, and the MacGillivray's Warbler used tall-willows (Table 1). These non-overlapping ranges afford ecological isolation through habitat segregation.

Cody's (1974) investigation of avian distribution in willow habitats near Jackson Hole, Wyoming, included several species common to this study. He reported that territories of Song Sparrows, Lincoln's Sparrows, and Common Yellowthroats occurred in low-structured willow vegetation and that those of MacGillivray's Warblers and White-crowned Sparrows occurred in patches of tall willow. The structural aspects of Yellow Warbler territories were intermediate between those of the Common Yellowthroat and MacGillivray's Warbler. Our results are consistent with Cody's findings, as well as displaying the relationship between soil moisture and vegetative composition. The Brown-headed Cowbird was not correlated with either CCA axis. Its central position in Fig. 5 indicates an indiscriminating distribution with respect to the habitat gradients. Brown-headed Cowbirds are brood parasites and have been reported to lay eggs in the nests of 214 species (Friedmann 1971). Their nonspecific distribution in the riparian habitat may represent a relatively general search for host species nests and/or broad habitat tolerance.

Extending the RA analysis into two dimensions improved interpretations of avian-habitat associations. Species overlapping along one resource axis may have clear ecological separation if additional axes are considered (Pianka et al. 1979). The Yellow Warbler had a broad distribution across the first RA axis. The second RA axis revealed its use of willow-dominated communities, thereby distinguishing it from species associated with coniferous habitats.

The second RA axis contrasted vegetative characteristics of the riparian region (conifer vs willow dominance). Both vegetative structure and species composition, which are not independent variables, are reported to influence avian habitat use (Rice et al. 1984). This study used structural aspects of the habitat by measuring foliage volumes of each lifeform (conifer, willow, forb, graminoid) at various strata. Although structural aspects alone (especially the vertical profile) correlate with avian distri-



bution in many habitats (MacArthur and MacArthur 1961, MacArthur et al. 1966, Anderson and Shugart 1974, Erdelen 1984), distinguishing structure with respect to lifeform improved the resolution of avian-habitat associations without adding excessive variables into the multivariate analyses (Johnson 1981b).

The RA and CCA analyses produced very similar structuring of the riparian habitat. This was interesting because RA constructed the habitat axes based on habitat data only, but CCA derived habitat axes under the constraint that they were maximally correlated with avian abundance. Both analyses supported the relationship between the avian distribution and the primary gradients within the riparian habitat.

Analyses of between-year variations in avian distributions considered variation due to observers (Faanes and Bystrak 1981) and to sampling intensities (Scott and Ramsey 1981). The 1983 data were collected during an "early season" period (8 June to 21 July), while in 1984 the censusing was during a "late season" period (5 July to 2 September). These sampling differences were unavoidable due to changes in spring snow cover between years. For several bird species, studies have shown that habitat use varies across seasons (Rice et al. 1983, Anderson and Ohmart 1983, Anderson and Ohmart 1985, Hutto 1985) and that detection may also change (Best 1981). Thus, the more extensive exploitation of tall-willow/xeric habitats in 1984 by the Western Tanager, Red-naped Sapsucker, and Yellow-rumped Warbler may be due to seasonal shifts in habitat use and/or sampling detection.

Although riparian zones are often considered a single discrete type of wildlife habitat (Thomas et al. 1979), our data indicate that there are distinct regions within the riparian zone with characteristic avian species use. If the relative position of a site along a habitat gradient were changed, the avian species using that site would be expected to change. Altering the dispersion of water within a riparian zone may be the most dramatic management practice affecting future plant and animal communities. Construction of dams and holding ponds, stream channelization, altering stream courses, and introduction or control of beaver populations are examples of environmental changes that alter soil moisture and, consequently, the avian community. Similarly, conifer, willow, or other lifeform dominance can be altered by vegetative changes associated with timber harvest, grazing, or fire.

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